hooks were fished on longline baskets with 9.1-m float lines, 2,160 hooks on baskets with 18.3-m float lines, and 2,340 hooks on baskets with 36.6-m float lines. No specimens were taken on longline gear with 9.1-m float lines. One *Taractichthys steindachneri* and seven *Taractes rubescens* were taken on longline gear with 18.3-m float lines. One *Taractichthys steindachneri* and three *Taractes rubescens* were taken on longline gear with 36.6-m float lines.

Saury and squid were used as bait on alternate baskets on each fishing station. More bramids were taken on hooks baited with saury than with squid. Nine *Taractes rubescens* were caught on hooks baited with saury, and two on hooks baited with squid. Both of the *Taractichthys steindachneri* were caught on hooks baited with saury. These results would indicate that fish constitute an important part of the diet of these bramids. However, only one of five stomachs (4 *Taractes rubescens* and 1 *Taractichthys steindachneri*) had fish remains. Squid and shrimp remains were more frequent in the stomachs.

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UPWELLING INDICES AND ANNUAL CATCHES OF DUNGENESS CRAB, *CANCER MAGISTER*, ALONG THE WEST COAST OF THE UNITED STATES[1]

The Pacific Coast Dungeness crab, *Cancer magister*, fishery shows yearly fluctuations in the catch. For example, since the 1948-49 season, the Oregon catch averaged 8.3 million pounds, with a range of 3.1 to 15.0 million pounds. Variations between seasons are characteristic of the fishery, however, long persistence of below average catches causes alarm in the industry. The years 1962-64 were such a period of low catches. The Pacific Marine Fisheries Commission (1964) noted that these fluctuations in abundance occurred uniformly along the entire west coast of the United States. Therefore, they concluded that some coast-wide environmental changes were responsible for the fluctuating crab catches.

Cleaver (1949) felt that the fishery had a strong dependence upon the survival of the young and that the abundance of the adult animals will fluctuate widely with conditions affecting the earlier stages. The Pacific Marine Fisheries Commission (1964) suggested that perhaps seasonal changes in water circulation patterns could sweep the pelagic crab larvae into unfavorable settling habitats, causing high larval mortality, thus accounting for fluctuations in abundance of the marketable adult crabs. Reed (1969) looked into the effects of temperature and salinity on survival of crab larvae. He concluded that these factors were unable to cause large fluctuations in larval survival.

Upwelling is a coastwide environmental phenomenon that varies from year to year. It has not been mentioned in any reports discussing the Dungeness crab fishery and its fluctuations. Yearly strength of upwelling is known to fluctuate (Hubbard and Pearcy, 1971). It is hypothesized that annual upwelling fluctuations are related to annual variations in fishery strength, since the west coast's resident commercial species (bottom fishes, shrimp, Dungeness crab, and mollusks) must depend in large part upon the increased food production during summer upwelling for their growth and survival. If several years of poor upwelling occur in a row, there may be several years of poor commercial catches, after some lag time. The converse should be true as well, assuming food is limiting. This paper will examine these possibilities by attempting to relate catches of Dungeness crab from the coasts of Washington, Oregon, and northern California to an upwelling index.

Certain aspects of the crab fishery make it uniquely suited for direct comparison to coastal upwelling. At the winter start of any crab fishing season, a finite number of legal-sized male crabs exist. The season essentially ends when virtually all of these animals are harvested. Tagging studies at Grays Harbor, Wash., in 1947 and 1948 found that minimally 79 and 87%, respectively of the available males were harvested (Cleaver, 1949. In California, research has indicated (Pacific Marine Fisheries Commission, 1964) that between 90 and 100% of the male crabs have been taken annually since 1928 or 1929. I am assuming that the intensity of the Oregon fishery has been similar. The Pacific Marine Fisheries Commission noted in 1964 that " . . . a few years ago, it took probably seven months to remove 90-95% of the available crabs. Now it takes hardly seven weeks." Fishing effort data are not required, since very few of the available animals escape capture. Therefore, total pounds landed in a given season is an excellent indicator of population size and possibly growth rate.

Reproduction is unaffected by the fishery, since males have several opportunities to mate, and females are not legally harvested. In Oregon and Washington, reproduction can occur at age 2. By age 3 probably most males have mated at least once during the summer mating season (Cleaver, 1949). These animals may reproduce again the following summer before entering the winter fishery at age 4½ yr. In California, mating occurs earlier, during late winter and spring. Males 1½ yr old have been observed mating, but generally do not until 2½ yr of age. At age 3½ males enter the fishery (Poole and Gotshall, 1965), 1 yr earlier than Washington and Oregon crabs. All along the west coast, females rarely, if ever, attain the legal size for males of 6¼-inch carapace width, and thus they are not generally retained in crab pots. The crab population may even be benefited by removal of those 4-yr-old males who have fulfilled their copulatory obligations, since this may reduce intraspecific competition for food required by growing 2- and 3-yr-old males, and egg-bearing females.

Coastal Upwelling and Dungeness Crabs

Ekman's theory (Bakun, in press) states that the net mass transport of water set in motion by sea surface winds will be 90° to the right of the direction in which the wind is blowing, in the northern hemisphere. The intensity of this water transport (referred to as Ekman transport) is a function of the intensity and duration of the wind stress.

Along the Oregon coast for example, winds generally blow from the north and northwest from April to September. The effect is a transport of surface water away from the coastline. This offshore near-surface transport is balanced by an onshore deep transport of cool, nutrient-rich water, coming to the surface. This phenomenon is called upwelling.

Strong upwelling off Oregon occurs when strong winds have a northerly component. The opposite phenomenon, downwelling, can occur if the winds have a southerly component. In this case warm surface waters are carried onshore, and cooler deep water moves offshore. Both phenomena occur in any given summer. The result of continuous steady northerly winds would be a summer of strong upwelling. A relative increase in the frequency of weak northerly and/or southerly winds would result in a summer of weak upwelling.

There is evidence that one of the biological effects of upwelling (i.e., increased production of copepods) is felt primarily along a rather narrow band paralleling Oregon's coastline, only a few miles wide, in close proximity to the shore. Zooplankton samples collected with fine-mesh nets off Newport, Oreg. (lat. 44°40′N), during periods of upwelling show the greatest abundances of phytoplankton and microcopepods at stations 1, 3, and 5 nautical miles from the beach. Microcopepod numbers drop rapidly farther offshore. Dungeness crabs are found only on sandy bottoms within this food-rich area of intense upwelling, from the 4-m contour out to about the 75-m contour (about 10 nautical miles offshore). The fishery is usually confined to less than 50-m depth (Waldron, 1958). If crabs are dependent upon food produced in the pelagic environment, their survival and thus their fishery may be influenced by annual variations in upwelling and food production.

Materials and Methods

Bakun (in press) has generated quantitative indices of upwelling based upon monthly mean wind stress on the sea surface at points near the coast. The indices are calculated for each 3° of latitude ranging from Baja California (lat. 18°N) to the Gulf of Alaska (lat. 60°N). Knowing wind stress one can compute the expected offshore Ekman transport and resolve the component of Ekman transport perpendicular to the coast. Bakun's data are derived from analyses of monthly mean atmospheric pressure fields, rather than from numerous but generally spotty direct wind observations. For an explanation of the methods used to convert pressure fields into geostrophic wind fields, see Bakun (in press).

The magnitude of the offshore component of the Ekman transport is considered by Bakun to be an index of the amount of water upwelled to replace that driven offshore. Negative values of the index are possible and indicate net onshore transport of water (downwelling) for that particular month. Negative values occur only during the winter months. A low positive value would indicate either weak offshore transport or alternating periods of upwelling and downwelling within that particular month. Positive values occur during summer months, and some spring and fall months. Maximum positive values (i.e., most intense upwelling) occur in July at all points north of San Francisco. I will refer to the upwelling season as the summer upwelling season since monthly indices are highest in June, July, and August.

Data on total pounds of Dungeness crab landed in Oregon and Washington were taken from the annual reports of the Pacific Marine Fisheries Commission (1959-70). The pre-1959 data were read from graphs in the same reports. Northern California data were taken from annual reports of the California Department of Fish and Game (1948-70). Data for 1970-71 and 1971-72 seasons were obtained from C. Dale Snow, Oregon Fish Commission (pers. comm.).

Monthly upwelling index data were summed for those months representing the upwelling season (as defined by Bakun) at the selected latitudes. These months are the only ones which may have positive values of the index. In some years, negative values occurred during certain spring and autumn months. Nevertheless these negative values are included in the summed upwelling season index. For Washington, upwelling indices calculated for lat. 48°N, long. 125°W were used. The May through September values were summed, thus generating an upwelling-season index. For Oregon, indices for lat. 45°N, long. 125°W were summed over April through September. For northern California, indices calculated for lat. 42°N, long. 125°W were summed over March through September. Only the California data representing the Eureka region will be considered here because the San Francisco region crab fishery has apparently collapsed since the 1961-62 season, as will be shown later.

Although upwelling index data are available for as early as 1946, west coast crab data for only as early as 1948-49 are considered because of the nature of the Oregon data. Until the 1948-49 season, both males and females could be harvested in Oregon, at 6-inch carapace width. Since then, only males of 6¼-inch carapace width have been legal. Therefore to make all data sets comparable, the 1948-49 season was chosen as the starting point.

Results

Figure 1 is a plot of crab catches in Washington. Oregon, and the Eureka and San Francisco regions of California. Since 1954-55, seasonal catch trends are quite similar for all three states. In each state, a trend of declining catches over the seven seasons from 1957-58 until 1963-64 is apparent, with the exception of high catches in northern California from 1958-59 through 1960-61, and in Oregon for 1959-60 and 1960-61

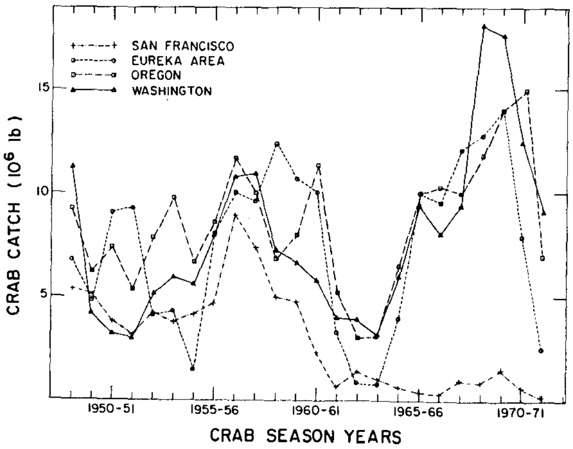

FIGURE 1.—Crab landings, in millions of pounds, for Washington, Oregon, northern California (Eureka area), and San Francisco area, by season, for the 25-yr period 1947-48 through 1971-72.

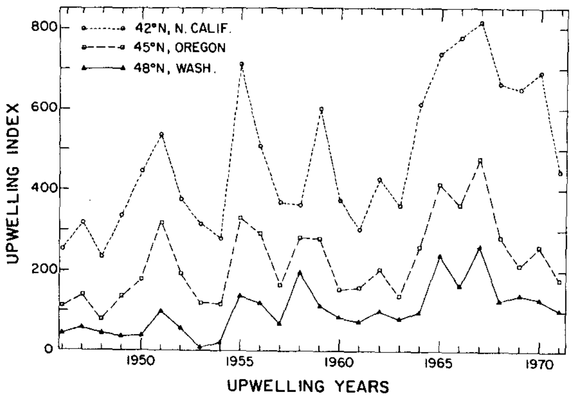

FIGURE 2.—Bakun's upwelling indices for Washington, Oregon, and northern California. The units of the index are cubic meters of water upwelled per second per 100 m of coastline. The northern California values represent summed March through September index values calculated by Bakun for lat. 42°N. The Oregon data were summed over April through September at lat. 45°N and the Washington data were summed over May through September at lat. 48°N.

seasons. The latter resulted from high catches in newly exploited crab grounds off Brookings, Oreg. (Pacific Marine Fisheries Commission, 1960, 1961). Perhaps the high catches in northern California during the same period were due to exploitation of these or other newly discovered beds.

The coastwide trend from 1963-64 until 1969-70 has been one of steadily improving catches climaxing in record catches for nearly all areas. What might have been termed a collapse of the Eureka and San Francisco region fisheries in 1962-63 and 1963-64 has become a reality for the San Francisco area ports. All other areas recovered from this depressed period.

Figure 2 shows the summed upwelling index values for lat. 48°N, 45°N, and 42°N. The units of the indices are cubic meters of water upwelled per second per 100 m of coastline. Absolute values of the indices were always lowest in Washington, intermediate in Oregon, and highest in northern California.

A uniform coastwide pattern of annual variability of the upwelling index is apparent in all three states, over the periods of 1948-57 and 1960-71. No coastwide trend is apparent for the summers of 1958 and 1959. Deviations from the agreement pattern do appear in other years (1949, 1954, 1961, 1966, 1969, and 1970) but they are small and probably insignificant.

Figures 3, 4, and 5 are time-series plots of upwelling index and crab catch, in Washington, Oregon, and northern California, respectively. Washington winter crab catches are plotted opposite the preceeding summer's upwelling index (½-yr lag). Oregon and northern California crab catch data are plotted with a 1½ yr lag (upwelling plotted opposite catch of the winter 1½ yr later). Reasons for the differing lag times will be discussed later.

The Oregon data (Figure 4) follows trends in upwelling index values remarkably well, since 1955. Notable is the weak upwelling period of 1960-63 followed 1½ yr later by the poorest crab catches in 1961-62 through 1964-65, and the high values of the upwelling index in 1964-68 followed 1½ yr later by record and near-record crab landings in 1965-66 through 1970-71. The record catch of 1970-71 would seem anomalous but very likely reflects the long-term effect that prolonged periods of very strong upwelling can have on the population. The three record years of upwelling in 1965-67, as well as strong upwelling in 1968, may have generated enough food reserves to keep the crab population supplied with a food surplus, thus contributing to a good catch 2½ yr later.

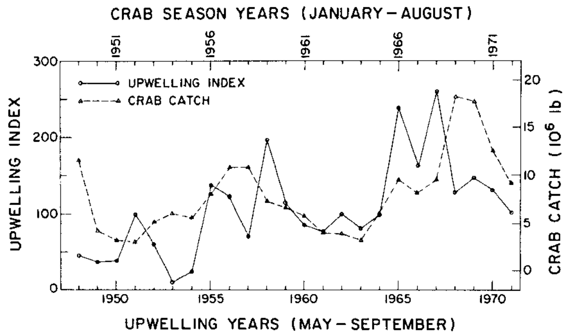

FIGURE 3.—Upwelling index values compared with crab catch in Washington. Crab catches are plotted opposite summer upwelling ½ yr earlier.

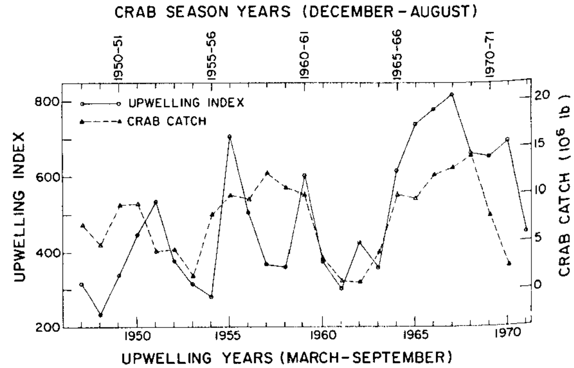

FIGURE 5.—Upwelling index values compared with crab catch in northern California. Crab catch is lagged 1½ yr.

The northern California upwelling-crab data (Figure 5) have paralleled Oregon's since the summer of 1959. The upwelling data for the summers of 1949-55 would match crab catch better if the crab data were lagged ½ yr (i.e., crab data shifted to the right 1 yr) instead of 1½ yr. The high crab catches of the 1958-59 and 1960-61 seasons may have resulted from exploitation of newly discovered crabbing areas, as suggested earlier.

In Washington State (Figure 3) trends are not apparent in the 1949-59 data set, but from the 1960-61 fishing season until 1971-72 the trend is similar to Oregon's trend.

Each upwelling-crab catch data set can be tested statistically for associations between the magnitude of the upwelling index and crab catch. Scatter diagrams of upwelling index vs. crab catch were prepared for lagtimes of ½ to 4½ yr for Washington and Oregon, and ½ to 3½ yr for northern California. (California crabs mature 1 yr earlier than those from more northerly points (Poole and Gotshall, 1965).)

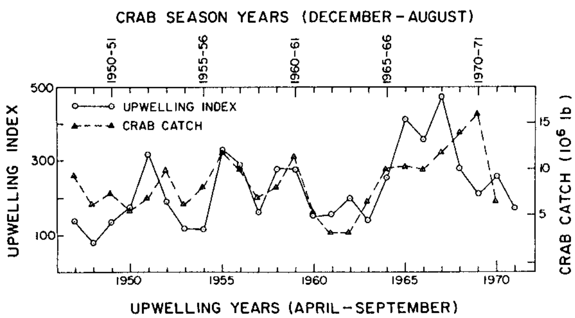

FIGURE 4.—Upwelling index values compared with crab catch in Oregon. Crab catch, in millions of pounds, is plotted opposite upwelling 1½ yr previous.

Figure 6 is Oregon's set of upwelling-crab catch scatter diagrams for the indicated lag times. (The Washington and northern California scatter diagrams are not illustrated but results of statistical tests performed upon the scatter are summarized in Table 1.) The median values of the upwelling index and crab catch partition each scatter diagram into quadrants. The first and third quadrants (upper right and lower left) represent strong upwelling-good crab catch and weak upwelling-poor crab catch, respectively. The second and fourth quadrants contain data points with the inverse relationship.

A number of statistics can be applied to these scatter diagrams to test the null hypothesis of independence, i.e., no relations between upwelling and crab catch. One of the tests is the corner test (Tate and Clelland, 1957:67). This test is useful in exploring general associations in a scatter diagram. Results of the test (Table 1) indicate that at the 5% level, a significant association exists between upwelling and crab catch ½ yr later in Washington, 1½ and 2½ yr later in Oregon, and ½, 1½, and 2½ yr later in northern California. Such a close time link between an environmental factor (upwelling) and its hypothesized effect upon a fishery implies that the fishery is dependent upon survival of older individuals, rather than juvenile individuals.

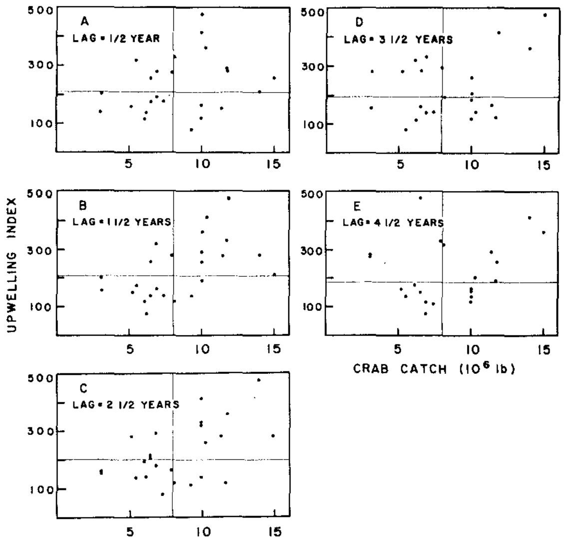

FIGURE 6.—Scatter diagrams of upwelling and crab catch for various lag times, for Oregon. The median values of upwelling index and crab catch divide each scatter diagram into quadrants.

The null hyphothesis of independence cannot be rejected for lag times of from 1½ to 4½ yr in Washington, 3½ and 4½ yr in Oregon, and 3½ yr in northern California. Nonsignificance at lag times of 4½ yr in Washington and Oregon and 3½ yr in northern California implies that the crab fishery is not strongly dependent upon the survival or growth of recently metamorphosed crabs, or upon the survival of crab larvae. Thus, even if abundance and survival of crab larvae in one year are important to a successful crab fishery some years later, upwelling has no strong influence upon these factors.

Another statistical test lends stronger support for this conclusion. Contingency tables (2 × 2) were set up from each scatter diagram. The tables were defined by the number of data points in each quadrant. For example, the 1½-yr lag scatter diagram for Oregon (see Figure 6) reduces to a

3	9
9	3

median value of crab catch

median value of upwelling index

TABLE 1.—Results of certain statistical tests performed upon scatter diagrams of upwelling index vs. crab catch in Washington, Oregon, and northern California. The Corner Test was performed on the scatter alone, while the absolute probabilities were calculated from 2 × 2 contingency tables set up from each scatter diagram. Quadrants were defined by the median value of the upwelling index and crab catch. The number of data points in each quadrant were the frequencies entered in each cell of the contingency table. The null hypothesis tested was independence of crab catch from the upwelling index. The absolute probability calculations indicate rejection of this hypothesis for the 1½-yr lag periods in Oregon and northern California, and the ½-yr lag period for Washington; i.e., crab catch and upwelling index are related at these lag times.

State or region	Lag time (Yr)	Corner test: Sum	Corner test: Level of significance	2 X 2 contingency tables: *A*	*B*	*C*	*D*	Absolute probability
Wash.	½	18	0.01	2	10	10	2	0.003
	1½	8	>.10	4	8	8	4	.22
	2½	7	>.10	4	8	8	4	.22
	3½	6	>.10	4	7	8	4	.22
	4½	5	>.10	5	6	6	5	1.00
Oreg.	½	10	~.08	4	8	8	4	.22
	1½	17	.01	3	9	9	3	.04
	2½	11	.05	4	8	8	4	.22
	3½	8	>.10	5	6	6	6	1.00
	4½	5	>.10	4	7	7	4	.39
N. Calif.	½	14	.01	4	8	8	4	.22
	1½	15	.01	3	9	9	3	.04
	2½	10	~.08	6	6	6	6	1.00
	3½	4	>.10	6	6	6	5	1.00

contingency table, symbolically represented by

A	*B*
C	*D*

Where $N = A + B + C + D$.

The chi-square test can be applied to contingency tables but the results tend to be unreliable when N is less than about 40 ($N = 24$ in my examples). In such cases, if reliable results are desired, the exact probability of a particular contingency table given the null hypothesis can be calculated from

$$P_0 = (A + B)!(C + D)!(A + C)!(B + D)! \div N!A!B!C!D!$$

(Tate and Clelland, 1957:73). To obtain a twotailed significance level, P_0 and the probabilities of each more extreme table with the same row and column totals which might have occurred, are summed and multiplied by 2. For example, the significance calculation for the 1½-yr lag table, for Oregon, is

$$P_0 \;\begin{array}{r|l} 3 & 9 \\ \hline 9 & 3 \end{array} = 0.0179 \qquad P_2 \;\begin{array}{r|l} 1 & 11 \\ \hline 11 & 1 \end{array} = 0.0006$$

$$P_1 \;\begin{array}{r|l} 2 & 10 \\ \hline 10 & 2 \end{array} = 0.0016 \qquad P_3 \;\begin{array}{r|l} 0 & 12 \\ \hline 12 & 0 \end{array} = 0.0001$$

where significance level, $\alpha = 2(P_0 + P_1 + P_2 + P_3) = 0.0404$. The significance levels for different lag times for all three states are presented in Table 1. (The null hypothesis of independence was rejected at the 5% significance level.)

The results indicate that crab catch and upwelling are related as hypothesized. The relationship is that summers of strong upwelling generally produce a good crab catch 1½ yr later along the coasts of northern California and Oregon. Along the coast of Washington, summers of strong upwelling almost always produce a good crab catch the following winter. The converse is also true (weak upwelling results in poor crab catches). It must be emphasized here that a qualitative statement is all that these statistics will allow.

Discussion

The observed lag times probably are a direct result of slow energy transfer through the pelagic environment to the benthos. The benthic predators may not experience upwelling-induced increases in food resources until many months after the onset of upwelling. Stephens, Sheldon, and Parsons (1967) determined that deposition of phytogenous material did not occur until 2 months after commencement of the annual spring phytoplankton bloom, in Departure Bay, British Columbia. Several times the generation time of the dominant copepods would be required after commencement of the bloom before copious amounts of fresh copepod faecal material would begin settling to the sea floor. Population increases of the benthic filter feeders and deposit feeders would lag additionally by the generation time of each species. Some of these animals (amphipods, polychaetes, clams, and shrimp) are known Dungeness crab prey. Other preys include small fish and small crabs (MacKay, 1942; Waldron, 1958).

Two-year old and older crabs moult annually. This event occurs during the summer off northern California, late summer-early fall off Oregon, and late fall off Washington (Poole and Gotshall, 1965, for northern California; Snow, pers. comm., for Oregon; Cleaver, 1949, for Washington). It is hypothesized that the California and Oregon crabs moult before benefitting from increased food resources, so their response to a summer of strong upwelling is not exhibited until the next summer's moult. Washington crabs however moult several months after the end of the upwelling season, and therefore must benefit from the increased production since the lag between strong upwelling and a good fishery is only ½ yr.

This hypothesis implies that a summer of strong upwelling off California and Oregon serves to maintain a large crab population throughout the coming year by both increasing food availability and decreasing competition for the food. Although lower food availability resulting from a summer of weak upwelling implies increased competition for food, increased mortality of sublegal adults need not be the only outcome of such competition. Another possibility is decreased moulting success. If a crab has not accumulated enough food reserves during a year of feeding, it need not shed its carapace. Numerous workers have observed from tagging studies and observations on the degree of fouling of the carapaces that Dungeness crabs can wait 2 yr before moulting (MacKay, 1942; Cleaver, 1949; Waldron, 1958; Butler, 1961; Snow and Wagner, 1965; Poole, 1967). The prevalence in the field is unknown. Poole (1967) believes that as many as 10-15% of the male crabs may miss moults. If moults are missed, animals would not enter the fishery until an additional year later, i.e., 1½ yr after a particular upwelling season in Washington and 2½ yr after in Oregon and California.

Graphically, I have shown (Figures 3, 4, 5) that trends of annual variability of crab catch were closely correlated with trends of annual variability of an upwelling index, for the period 1959-71. Poor correlations during the period 1950-58 may have resulted from one or a combination of at least four causes. First, if the fishery were not as intense in these earlier years so that fewer than 90-95% of the available males were taken during a particular season, each seasons catch may be higher than an upwelling index might suggest. Second, if at any time during this period some previously unexploited areas were fished, the statewide catch data would be higher than one might predict, if one could predict catch. For valid comparison of the raw catch data to environmental factors, all crab beds must be "cleaned-out" each year. Third, the upwelling index may be in error during this period. Earlier atmospheric pressure data may not be as reliable, or sparce data coverage may have yielded erroneous indices. A fourth alternative may be that all data are adequate, and that only the extreme conditions influence crabs. Four summers of poor upwelling occurred together from 1960 to 1963, followed by five summers of good upwelling in 1964-68. Crab catch trends were well established during this period. Prior to the 1960's no such persistent trends were found, except with the Oregon data.

To my knowledge, this study represents the first published attempt to relate Bakun's (in press) upwelling index to fisheries data. Although the physical meaning of the index is clear (index value proportional to the volume of water upwelled) it must be remembered that it expresses a monthly mean condition. A low value of the index does not necessarily imply that upwelling-induced production was low in a particular month. For example, if during a particular month, there were 5-day periods of alternating northwest and southwest winds, the upwelling index would be low, but biological production may still have been reasonably high. In this light then, perhaps only persistent summers of either high or low values have biological meaning.

Whatever the reasons might be for certain anomalous data points occurring during the period 1950-58, the data from the past 13 yr lend strong support to the hypothesis that upwelling is responsible for fluctuations in the crab catches of the west coast, and that the catches show response to the upwelling 1½ yr later off northern California and Oregon, and ½ yr later off Washington.

Acknowledgments

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